Investigating the life history strategy of an African savanna tree, *Sclerocarya birrea* subsp. *caffra* (marula)

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Abstract

Lack of understanding of the life history attributes and responses of savanna woody plants to disturbances, as well as the observation of unstable population structures in a keystone, savanna tree*, Sclerocarya birrea* subsp. *caffra* (marula), prompted this study. This study employed a combination of empirical, experimental and model formulation techniques, aimed at achieving its ultimate purpose of understanding the life history strategy of marula in the face of disturbance. Four main population structures were identified for marula in the low altitude savannas of South Africa: 1) adult dominated, 2) juvenile dominated, 3) with a "missing size class" and 4) stable (negative J-shaped). Spatial variability in structure indicated different drivers affecting different populations. High annual mortality rates of up to 4.6% in adult trees, no recruitment out of the fire trap and little regeneration were observed in the Kruger National Park (KNP) between 2001 and 2010, and consequently even greater instability in the structure of these populations already observed earlier in the decade.

Growth rates of saplings between 2 and 8 m in height and 2 and 30 cm in stem diameter in the field were monitored between 2007 and 2010. Annual growth rates of up to 11 mm in diameter and up to 22 cm in height were observed. Annual relative growth rates ranged between 1.9 and 4.8% across sites. Growth rates were positively linked with rainfall and plant size. Growth rates, biomass allocation patterns, as well as storage and defence allocation in 3 to 28 month old marula seedlings were assessed under glasshouse conditions. Relative growth rates were highest directly after germination (20%), but did not exceed 5% thereafter. Allocation to roots (already 65% of the overall biomass at 3 months of age and >80% when older) was high regardless of soil type or provenance. Provenance affected height gain, and plants germinating from seeds collected at higher rainfall sites had faster height growth rates than those from seeds collected at lower

rainfall sites. Allocation to storage in the form of root starch peaked at 35%, while allocation to defence in the form of phenolics in the leaves peaked at 18%, being relatively higher than other species. No trade-off between growth and defence allocation was observed. However, in the second growing season, growth at the start coincided with a 50% decrease in starch reserves in the roots. Reproductive maturity was found to occur after 46 years and escape from the fire trap after 12 years in a disturbance free environment. Marula trees appear to be able to live for up to 300 years of age.

High temporal variability in fruit production was observed, marginally linked to rainfall. Only 2% of seeds persisted for more than one year, and hence marula relied mostly on the current season's fruit crop for input of new germinants. Fruit production was highly synchronous across trees at a site. Very high levels of seed predation were observed. Marula seeds can remain dormant for at least 10 years when stored in the laboratory. Germination takes place after 3 mm of rainfall every four days for two weeks and is enhanced by acid digestion and high temperatures. Germination percentages are relatively low (<50% of the endocarps).

Marula seedlings appear highly adapted to fire, with high allocation to below-ground biomass and starch storage, as well as very thick bark from very small stem diameters, including a well developed resprouting response from very young. Marula stems were able to resist fire from 3.4 cm in stem diameter, and were completely resistant above 7 cm. Stem diameter growth was prioritised above stem height growth, indicating that in marula, diameter gain is more important than height gain in escaping the fire trap. Topkilled marula saplings are able to regain their prefire height within one season. However, rainfall patterns may have an overriding effect on these growth patterns. Adult trees appear to be made vulnerable to fire through bark stripping, toppling and pollarding and the subsequent invasion of the soft wood by borers.

On nutrient-poor granite soils, marula has a resistant strategy to herbivory, however on nutrient-rich basalt soils, marula overcompensates for herbivory even at very low levels. This may explain why marulas are more vulnerable on basalt soils in the KNP, having

already been extirpated from the northern arid basaltic plains. Marula seedlings are extremely drought resistant through fast root penetration rates and high root: shoot ratios.

A simple demographic model was developed which predicted that marula populations are unlikely to survive given the current elephant impact in the KNP and if the fire interval is less than once every seven years. Even though marula is highly resilient to damage from herbivory or fire alone, the combination of frequent fire and heavy utilisation is proving fatal for marula populations in the KNP and elsewhere.

In terms of other savanna tree species, marula is an outlier in its life history strategy, being extremely well adapted to the effects of fire with very thick bark, extensive resprouting ability and fast growth rates, combined with very high allocation to root mass, and levels of storage and chemical defence, as well as having very drought tolerant seedlings. Its main weakness as an adult, appears to be its soft wood, which is susceptible to wood borer attack. The perplexing lack of recruitment at some sites in spite of the extraordinary ability of marula seedlings to resprout from an early age, withstand extensive drought, have fast root penetration rates, extremely high root reserve storage and resistance to fire at small stem diameters, combined with high levels of fruit production and low water requirements for germination, is probably due to a combination of the lack of a dense persistent seed bank, high inter-annual variability in fruit production, low germination percentages, high seed and /or seedling predation rates and possibly dispersal of seeds away from suitable habitats. Overall, the unstable population structures observed in the low altitude savannas of South Africa, specifically in the KNP, do not bode well for the future persistence of marula as a dominant canopy tree species.

Keywords: elephant, fire, growth, mortality, recruitment, regeneration